AN ACCOUNT OF *PLAGIORCHIS MACULOSUS* (RUD.), ITS SYNONYMY AND ITS LIFE HISTORY IN SOUTH AUSTRALIA

by MADELINE ANGEL*

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SUMMARY

A historical account of the parasitic trematode *Plagiorchis maculosus* (Rud.) since its description in 1802 is given.

An amended diagnosis of the species is given.

It is recorded from South Australia from the birds *Hirundo neoxena*, *Rhipidura leucophrys*, *R. flabellifera*, *Gymnorhina hypoleuca*, and *Pomatostomus superciliosus*. Two trematodes from *Grallina cyanoleuca* may also be *Plagiorchis maculosus*.

To avoid confusion in taxonomy, it is urged that authors give full details of treatment and fixation of worms. It is also desirable to know the age of the worm, and the number of specimens examined. Given details such as these, it is possible to make allowance for characters which may be variable.

Tables are given, showing measurements of *P. maculosus* recorded by different authors since Rudolphi; of other species which are discussed for synonymy; and of South Australian specimens which have been studied in the present investigation.

A history of knowledge of the life history is followed by an account of the life history in South Australia, in *P. maculosus* from swallows, wagtails, babblers and, experimentally, chickens.

A description of the various larval stages is given. The size of the stylet in the cercaria should not be used as a diagnostic character in this species.

The synonymy is discussed. *Plagiorchis clelandi*, *P. spatulatus*, *P. notabilis* and *P. orientalis* are given as synonyms. It is suggested that examination of the types of *Plagiorchis* sp. from insectivorous birds, or animals which (normally or accidentally) ingest insects, may reduce the number of species still further.

Plagiorchis russii is shown to be invalid, being a synonym of *P. potanini*.

The three varieties, *Plagiorchis maculosus anatis*, *P. maculosus citelli* and *P. maculosus motacillae*, are discussed. The variety *citelli* shows no differences from the typical form, and is made a synonym. If the large size of the testes is a uniform character, the variety *anatis* stands, with var. *motacillae* a synonym.

INTRODUCTION

In 1802, Rudolphi described *Fasciola maculosa* from the terminal part of the intestine of *Hirundo rustica*. He gave as synonyms *Fasciola hirundinis* Froelich (1791) and *Distoma hirundinum* Zeder (1800), from the rectum of *Hirundo apus* and *H. urbica* respectively, mentioning that, though their descriptions differed in many respects, the worm itself was very variable. In 1809 (p. 374) he referred to it as *Distoma maculosum*, and in 1819 (pp. 382-3) recorded it (by this name) from *Caprimulgus europaeus*.

The species was recorded or listed by various authors in the following century, but it was not until 1902 that an adequate figure was published, by Braun, who assigned the species to the genus *Plagiorchis* Lühe (1899).†

* Department of Zoology, University of Adelaide.

† On the same day that Lühe's generic name appeared, Looss published the name *Lepoderma* for the same genus. Lühe did not name the genotype till later, and it would seem that *Lepoderma* should have had priority. However, relatively few workers have used the name since that time, and *Plagiorchis* seems now commonly accepted, although Dollfus in 1949, referring to family Lepodermatidae, gave Plagiorchidae as a synonym.

Braun examined Rudolphi's specimens, which he stated had deteriorated over the years, so that the species could not be sufficiently described from these specimens alone. However, they corresponded with similarly named examples from the Vienna, Munich and Königsberg collections. He gave figures of the dorsal and ventral view of a specimen from *Hirundo rustica* from Königsberg. From the magnification given the worm would be $2 \cdot 7 \times 0 \cdot 8$ mm. Braun gave no real description of the species, but he referred to the variability in the size of the suckers (even among animals of the same size) and in the arrangement of the yolk glands.

In 1909, Lühe gave a key and a description of 6 species of *Plagiorchis*. As this was the first real description of *P. maculosus* to be published, a translation is given here:—

About 2·0-2·5 mm. long; 0·5-0·7 mm. wide; oval in cross-section. Oral sucker about 0·2-0·3 mm. Ventral sucker approximately at end of first third of body length; about 0·15-0·20 mm. in diameter. Pharynx smaller, and ovary usually somewhat smaller, than the ventral sucker. Yolk glands lateral, extending from the pharynx to the hind end of the body; only at the hind end spreading out to meet on the dorsal surface. Testes comparatively large, spherical, occupying about the third quarter of the body length. Uterus behind testes forming no clearly defined loops.

Braun's figure and Lühe's diagnosis seem to have formed the basis of subsequent identifications. Table II lists the measurements recorded for *P. maculosus* from many hosts since Lühe's time.

In 1929 Massino gave a key to 24 species of the genus. This was based primarily on the position of the testes and secondarily on the relative sizes of ovary and testes.

In 1931, Schulz and Skorzow proposed two subgenera for *Plagiorchis*, namely, *Plagiorchis* and *Multiglandularis*, according to whether the yolk glands do not meet in front of the ventral sucker, or join to form a marked commissure. *Plagiorchis maculosus* was placed in the subgenus *Plagiorchis*.

In 1937 Olsen published a study of the Plagiorchiinae, which included a key to the subgenera and species of *Plagiorchis*. There were 43 species and 2 subspecies. (Olsen also listed 4 species the descriptions of which were not available to him.) It would seem that many of the characters given in Olsen's key are subject to a good deal of variation within any one species, and the key is, therefore, not very satisfactory. In 1932 Schulz had expressed the opinion that a critical revision of the whole genus was necessary; *Plagiorchis* contained some 50 species from various orders of vertebrates, but specimens showed great variability, and a much-needed revision might reduce the number of species to 15 or 20. Other authors have shared Schulz's opinion of the desirability of a revision of the genus, but so far this has not been made.

There are now some 90 described species of *Plagiorchis*, and the number seems likely to grow unless authors will appreciate the necessity of allowing for some considerable amount of variation of characters within a species, whether due to differences in age, fixation or treatment, etc., and for the possibility that some species may occur in a more or less wide range of hosts.

Ulmer (1952), in a critique of methods for the measurement of parasitic worms, thought that much of the present-day confusion in taxonomic studies might be avoided if authors would state, as far as possible, the age of the worms, whether specimens had previously been flattened, and what fixatives were employed. Cover glass pressure may cause marked changes, not only in body size, but also in the shape and relationship of non-muscular organs, such as the genitalia, which are often of taxonomic importance.

Gilford (1955) examined 300 specimens of *Allassogonoporus marginalis*, and reported that the relative positions of internal structures of the worm change during growth. Flattening during preparation for staining also will alter size, shape and position of these structures.

Callot (1946) gave measurements for a living specimen of *Lepoderma maculosum* (Rud.), and for the same specimen, fixed. These figures are shown in Table 2. It will be noticed that though the size of the oral sucker remained unchanged, the ventral sucker was smaller in fixed than in living material. The pharynx, too, $140 \times 75\ \mu$ living, was only $75 \times 50\ \mu$ fixed.

One of the characters Olsen used in his key was the position of the oral sucker, which, according to the key, is sub-terminal in *Plagiorchis maculosus*. In his description, Rudolphi stated that the mouth aperture was terminal. Among 14 specimens collected from 7 swallows from Wellington, S. Aust., in March 1956, most showed the oral sucker terminal, but in at least one it was sub-terminal. It is clear from an examination of such a series, as well as of living animals, that the apparent position of the oral sucker may depend on the position and state of contraction of the animal at the time of fixation.

Again, too much stress should not be placed on the relative sizes of the organs (oral and ventral suckers, pharynx, ovary and testes) and of their positions in the body. Descriptions of trematodes have often been given from one, or very few, specimens, and the condition of the animal (whether living, compressed, etc.) is seldom stated.

The absence of a receptaculum seminis was given by Lühe (1909) as one of the characters of the genus *Plagiorchis*. Olsen (1937) put *P. noblei* Park, 1936 into a new genus (*Plagiorchoides*), on the grounds that it had a receptaculum seminis, and in the same year, for this and other reasons, Mehra transferred it to *Neolepoderma* n.g. In 1939, Park suggested that if the possession of a seminal receptacle is to be a generic character the study of serial sections is absolutely necessary for diagnosis. In 1943, Baer (p. 43) stated that the presence of a seminal receptacle was typical of the genus *Plagiorchis*; this was quoted by Dollfus (1949, p. 437) without comment.

Yamaguti (1954) recorded *P. maculosus* from single specimens, from *Sturnia philippinensis* and *Passer montanus* from Macassar. The specimen from the first host was examined as a mounted specimen; there was a prepharynx and a small receptaculum seminis, which suggests that the identification is doubtful. On the other hand, the excretory system was studied in the second specimen, living. The excretory formula was given as $2\{(2+2)+(2+2)\}=16$. If all the flame cells were observed, the specimen could not belong to *Plagiorchis*, in which the flame cell pattern is $2\{(3+3+3)+(3+3+3)\}$ (McMullen, 1937). However, flame cells are not easily seen, and with only one trematode to study, it is probable that some were missed.

The presence or absence of a receptaculum seminis seems thus to be a character of doubtful value. Without good serial sections, it would seem unwise to be dogmatic on its presence or absence in *Plagiorchis* species. It was not observed in the present investigation, although serial sections of two specimens (from swallow and wagtail) were studied.

The shape of the cirrus has been made a descriptive character, especially in the earlier accounts. Examination of a number of specimens of *P. maculosus* in the present investigation suggests that its apparent shape and size are variable, probably depending largely on the state of contraction of the animal, and the extent to which the cirrus is extruded. Fig. 1 shows a relatively broad cirrus, not greatly elongated; in most specimens in which it was everted, it was very narrow. One specimen (from a chick) showed the narrow cirrus projecting a distance of 245 μ from the genital pore; in another (from a swallow), self-fertilization was observed, the cirrus being inserted well into the metraterm.

From records of *Plagiorchis maculosus* (details of which appear in the foregoing pages and in the tables) and from observations recorded in the present paper, the following amended diagnosis has been compiled:—

Plagiorchis maculosus (Rud.)

Diagnosis—Mainly in insectivorous birds; also occasionally in other birds and in mammals. Snail host a lymnaeid; second intermediate host an insect with an aquatic larva.

Just under 1 mm.-4 mm. long; 0·4-1·25 mm. wide. Suckers about the same size, or oral sucker slightly larger than acetabulum. Acetabulum at end of first third of body length, or further caudad; well behind intestinal bifurcation. Prepharynx, if present, very short. Oesophagus present in cercaria; very short or apparently absent in adult. Intestinal caeca extend to near posterior end of body; wide, though not necessarily fixed in this position. Ovary smaller than acetabulum, or nearly equal to it; smaller than testes. Vitellaria extend anteriorly and laterally between pharynx and anterior border of acetabulum; posteriorly they extend to hind end of body, and fields may remain separate or may become confluent in mid-line.

The name *maculosus* was evidently given by Rudolphi for the testes and ovary—two or three "light spots" behind the ventral suckers which were especially characteristic for this worm. Other authors have attributed the name to the spination of the fore part of the body, and even to "the diffuse granules which remain from the eyes of the cercaria".

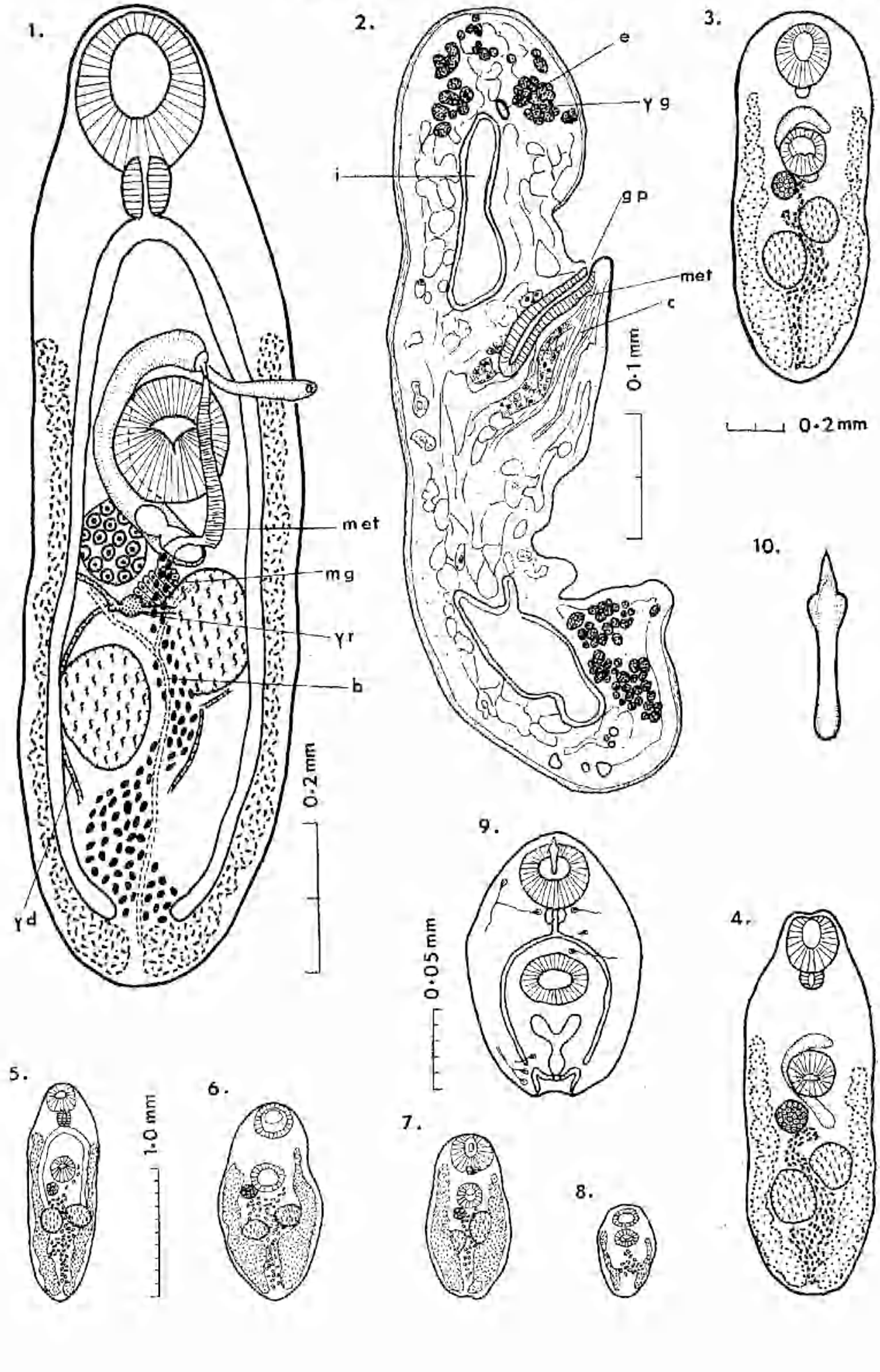
This trematode is now identified from South Australia from the swallow (*Hirundo neoxena*), the willy wagtail (*Rhipidura leucophrys*), the grey fantail (*R. flabellifera*), the magpie (*Gymnorhina hypoleuca*) and the white-browed babbler (*Pomatostomus superciliosus*). Measurements of the parasite from these hosts and from two chickens infected experimentally are given in Table 1. This table also includes measurements of two specimens of *Plagiorchis* from the Murray magpie (*Grallina cyanoleuca*). It is considered probable that they are *Plagiorchis maculosus*, but one specimen was not well preserved and does not look quite typical, and the other showed the ovary relatively larger than in specimens from other hosts. In the absence of further specimens from this host it is perhaps safer to identify these two trematodes as *Plagiorchis* sp.

Most of the specimens from *Pomatostomus superciliosus* did not resemble the typical *Plagiorchis maculosus* at first sight. They had been fixed, when alive, without any pressure; they were relatively short and stout, the anterior sucker was always subterminal, and the two suckers appeared to be placed close together, due to the curvature of the body. The skin was wrinkled and rather dark. In spite of this apparent dissimilarity it was not possible to name any essential differences, and sizes of organs conformed to the pattern of *P. maculosus* from other

EXPLANATION OF FIGURES

Fig.s 1-10. *Plagiorchis maculosus.* Figs. 1, 3, 4. Adults from swallow (March, 1956); N.B.—Variations in extent of vitellaria anteriorly, position of testes, oral sucker, etc.; 1, stained alum carmine. Fig. 2, T.S. Adult from wagtail, through genital pore. Figs. 5-8, Adults from babbler, 6-8 fixed alive, uncompressed; 5, fixed after death. Fig. 9, Cercaria; fixed specimen, position of some flame cells shown. Fig. 10, Stylet.

Fig. 4 is to the same scale at Fig. 3. Figs. 6, 7, 8 are to the same scale as Fig. 5. b, bladder; c, cirrus; e, excretory canal; g.p., genital pore; i, intestine; met., metraterm; m.g., Mehlis' gland; yd., yolk duct; yg., yolk glands; yr., yolk reservoir.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hosts, although the distances between organs was generally reduced owing to the contracted state of the specimens. A few of the trematodes from the same collection had been fixed after death (Fig. 5); they were extended, were not dark in appearance, and were much more like *P. maculosus* from other hosts.

Of 8 specimens obtained experimentally from chicks, 4 were dissected when alive to obtain the eggs, so that measurements of only 4 are given. The suckers of the dissected specimens were measured in formalin and are included in the measurements.

LIFE HISTORY

Historical

As early as the 1850's there were suggestions concerning the life history of *Distomum maculosum*. Filippi's *Cercaria virgula* (named in 1837), the sporocysts of which were found in *Valvata piscinalis* and *Paludina impura*, and which encysted in perlids and some other aquatic insect larvae, was suggested as the larva of *Distomum maculosum*. Filippi and Diesing both referred to this. I have not had access to all of Filippi's papers, but in 1901 von Linstow mentioned that Filippi (1857) assumed, and probably rightly, that *D. maculosum* was the adult of these larval forms. Diesing (1858) stated that whether *Cercaria virgula* was the true larva of *Distomum maculosum* was still sub judice.

These two molluscs belong to different families, neither of which is closely related to the Lymnaeidae. The more recent work of Nöller and Ullrich (1927), Strenzke (1952), and the present investigation has shown a lymnaeid to be the snail intermediary for *Plagiorchis maculosus*. It seems likely that Filippi was identifying two different cercariae in his *Cercaria virgula*, and that neither of them was the cercaria of *Plagiorchis maculosus*.

Von Linstow described thick-walled, oval cysts in the neuropteran, *Drusus trifidus*. The contained metacercaria agreed so closely with *Distomum maculosum* that he considered it belonged to this species. He gave a figure of the metacercaria which showed ovary, testes and cirrus, but no uterus. The figure certainly suggests *Plagiorchis*, but from the description of the cyst, as well as its size, it seems unlikely that the species is *maculosa*.

Nöller and Ullrich (1927) reported that a xiphidiocercaria of the "Armata" group, from *Limnaea stagnalis*, encysted in chironomid larvae. After adult and larval chironomids had been fed to canaries, finches and other small birds, trematodes identified as *Plagiorchis maculosus* were recovered. (35 mature trematodes were found in a canary on the 9th day.) Photographs of the various stages were given; though these do not show much detail, there is no reason (of appearance or size) to doubt that *P. maculosus* was the trematode involved. Although 7-week-old chicks were fed many larvae on successive days, none became infected. Nöller and Ullrich did not give a description of the sporocyst and cercaria, which they hoped to do later.

Strenzke (1952) gave an account of the life history and a description of the various stages of *P. maculosus* in Holstein. Sporocysts occurred in the mid-gut of *Radix auricularia*; the cyst was found as a natural occurrence in the larvae of *Chironomus thummi* and *Psectrotanypus varius*, and experimentally in larvae of the midge, *Chaoborus crystallinus*, and *Culex pipiens*. Two specimens of *Aidemosyne cantans* were infected (with 85 and 262 trematodes respectively) by feeding with infected chironomids.

Experiments in South Australia

On 5th March, 1955, 2 of 55 *Lymnaea lessoni* collected at Mannum (River Murray) were found to be infected with a small xiphidiocercaria. One of these snails was used for the following work.

The cercariae were found to encyst in mosquito larvae. From 8/3/55 the cercariae were put in small dishes each day with a batch of mosquito larvae. As the larvae and pupae died, or the adult mosquitoes hatched, they were fed to young chickens. Two of these chickens were later found to be infected with adult trematodes which were identified as *Plagiorchis maculosus*, and three were uninfected.* Most of the larvae could have contained several cysts, and some of them possibly many. The attempted infections of these five chickens may be summarised as follows:—

(1) Fed with 50 larvae; died 12 days after first, and 8 days after last larvae fed. No trematodes recovered.

(2) Fed with 81 larvae, etc.; killed 49 days after first and 40 days after last larvae fed. No trematodes recovered.

(3) Fed with about 250 larvae, etc.; killed 40 days after first and 25 days after last larvae fed. No trematodes recovered.

(4) Fed with 227 larvae, etc.; died 13 days after the first and 3 days after last larvae fed. Six adult trematodes recovered.

(5) Fed with 216 larvae, etc.; killed 21 days after the first and 14 days after last larvae fed. Two adult trematodes recovered.

The results from chicks (4) and (5) show that the trematodes had reached maturity within 13 days, and possibly less, after the cysts were ingested. (Stronzke fed finches with infected larvae and found trematode eggs in the faeces 7 days later. In one finch he recovered 85 trematodes, and in the second 262 specimens; the birds died as a result of the infection.)

The foregoing results suggest that chicks, not being the natural definitive host of *P. maculosus*, do not become infected unless given a massive dose of the cysts or that the infections are lost early.

The six *Plagiorchis maculosus* from chick (4) were left in saline from 4-8/4/55, and the eggs laid, with those dissected from three of the trematodes, were kept for a further seven days in boiled water, which was changed daily. No miracidia were seen during this time. On 15/4/55 the dish containing the eggs was put in a small infection tank with 12 young laboratory-raised *Lymnaea lessoni*. One snail was completely disintegrated when found, 32 days later. Of the remaining snails, 10 died, in 39, 42, 43, 45, 48, 48, 49, 53, 53 and 55 days. Sporocysts were found in all, tailed cercariae being present in those which died in 43, 48, 49, 53 and 53 days. The twelfth snail was isolated, for the first time, 56 days after it had been placed in contact with the eggs, and was found to be emitting cercariae; it died 8 days later.

Eggs from the two *Plagiorchis maculosus* from chick (5) were left at room temperature for 17 days before being placed with 9 young *Lymnaea lessoni*. It is not known whether the eggs were still viable. The snails died from 42 to 132 days afterwards, and none was infected.

Mosquito larvae were infected with cercariae from the infected snail. Only about 50 infected larvae were available to feed to two chicks when the snail died; the chicks were killed 7 weeks later, but were not infected.

Life history studies were also carried out with *Plagiorchis maculosus* from swallows, wagtails and babblers.

Eggs laid in normal saline were collected, and others were dissected from the adult trematodes. The eggs were kept in boiled water at room temperature during the week, and were examined daily when the water was changed. Over week-ends they were kept at 4° C.

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* Rees (1952, p. 93) noted that a mounted specimen of *P.* (*P.*) *maculosus* (from a turkey) in the Natural History Museum showed no differences from the same species recovered from the normal bird hosts.

Lymnaea lessoni reared in the laboratory were used. Dead snails were dissected under binocular microscope. Results are summarised below; the result "apparently negative" means that larval stages were not seen. (Records of deaths of snails which were too disintegrated for examination are not given.)

Pomatostomus superciliosus

Eggs laid 1-3/3/56; dissected 7/3/56; put with snails 9/3/56.

One snail apparently negative in 14 days.

Four snails had sporocysts, but no free cercariae, at 27, 33, 34 and 39 days.

Hirundo neoxena

Eggs dissected from 4 trematodes 14/3/56; put with 12 snails 22/3/56.

Three snails apparently negative when they died in 15, 21 and 21 days.

1 snail had sporocysts at 21 days.

One snail had numerous sporocysts and a few motile cercariae at 39 days.

One snail emitted cercariae when tested at 40 days. (It had not done so when previously isolated at 26 days.) Died at 43 days.

Rhipidura leucophrys

Eggs dissected from 6 trematodes 15/3/57; and from 2 trematodes 18/3/57; put with snails 22/3/57.

Three snails were dead and apparently negative at 17, 24 and 36 days.

Remaining 7 snails all gave abundant cercariae when first isolated at 45 days. (These snails died at 45, 46, 47, 48, 50, 69 and 73 days.)

The above results show that the shortest time observed for the production of cercariae was 39 days (in *L. lessoni* subjected to infection in March), and it seems probable that this was not much longer than the actual time taken for infections at this time of year.

Snails other than *Lymnaea lessoni* have also been used in experiments on a number of occasions. In the earlier experiments the trematode eggs were put with the snails within a day of being dissected from the trematode; although all results were negative, this cannot be regarded as significant, in the absence of *L. lessoni*, since it is probable that the eggs would not be infective for several days after being laid or removed from the adult. However, in March 1956, 8 *Amerianna* sp. did not become infected in 21, 25, 28, 36 and 64 (4) days, in the same tank in which 3 *Lymnaea lessoni* were infected with *Plagiorchis maculosus* from the swallow; and in the same month, 4 *Amerianna* sp. were uninfected after 56 and 62 (3) days, in the same tank in which 4 *Lymnaea lessoni* showed sporocysts as early as 27 days.

OBSERVATIONS ON STAGES IN LIFE CYCLE

The Egg and Miracidium

The eggs averaged about 30 $\mu \times 19\ \mu$, but the length varied from 29-31·5 μ, and the breadth from 17-20 μ.

There is no evidence as to the hatching of a miracidium. If there is a free-swimming miracidium, the experiments suggest that hatching does not occur earlier than 7 days after the egg is laid. Strenzke did not find a miracidium. It seems probable that hatching follows ingestion of the eggs by the snail host.

It was not possible to make out any detail in viable eggs under ordinary high power, though the miracidium was seen to move within the shell several days after the eggs were laid.

The Sporocyst

The sporocysts were small and contained only a small number of cercariae. They corresponded in appearance with that shown in Strenzke's photograph. Formalinised specimens measured up to 0·8 × 0·14 mm. in snails infected 46 days previously; while in snails infected 39 days previously the largest sporocyst observed was 0·54 × 0·14 mm. Strenzke's figures were 0·7-1·0 mm. × 0·20-0·25 mm.; his measurements were probably of living material and in newly killed snails. In the present investigation sporocysts were not examined until the snail was found dead, and under these circumstances most of the cercariae have escaped from the sporocyst, leaving it thinner in appearance. As shown by the dimensions above, the size is probably also dependent to some extent on age.

The Cercaria

The cercaria has been found as a natural infection of *Lymnaea lessoni* from the River Murray swamps, from Wellington to Morgan, in 73 of over 8600 of the snails examined between April 1937 and March 1958 (0·85 per cent. infection). It has also been found in a small pond in a garden at Tailem Bend in 57 of 1700 *L. lessoni* since 1943 (3·3 per cent.).

The cercariae emerged normally in the early morning (before 9.30 a.m.). Their activity diminished noticeably during the morning, and by afternoon only a few were still swimming; the remainder were still alive, but lying at the bottom of the tube. About 4 p.m. some cercariae were put at 5° C., and 24 hours later, when brought out to room temperature, they swam quite actively.

Measurements of cercariae collected at different times from naturally infected individual *L. lessoni*, as well as from *L. lessoni* which had been experimentally infected with eggs from different bird hosts, are given in Table 3. They were fixed by adding an equal volume of boiling 10 per cent. formalin to the water in which they were swimming. It will be noticed that there is a slight variation in size range for the cercariae from individual hosts. This is regarded as being of no significance, considering the number of variable factors involved. The cercariae were deliberately chosen for measurement from those which had been fixed in the most extended position. The time of day at which they are killed is likely also to affect the state, whether extended or otherwise.

Strenzke gave the following measurements for cercariae "killed by slight heating". Length 250-300 μ; breadth 120-140 μ; diameter of oral sucker 60 μ, ventral sucker 36 μ.

The size of the stylet in this particular cercaria is somewhat variable. The stylet is also rather fragile in formalin, and splits lengthwise under even moderate pressure of a coverslip. It was difficult with almost all the formalinised material to find an adequate number of stylets which were in good condition and also in a suitable position to be measured accurately. The actual range for length of formalinised stylets was 21·5-24·8 μ,* in the comparatively small number measured, while for living specimens it was 24·3-28·9 μ. In all cases measurements on stylets of living cercariae were greater (by 1·2-3·8 μ) than on stylets of formalinised cercariae from the same snail. Strenzke gave a measurement of 25-27 μ, and this would probably be the normal range in our material, though larger and smaller specimens do occur. Precise length of stylet should not be used as a diagnostic character for *Plagiorchis maculosus*.

The stylet is shapely, 6-7 μ across the shoulders, the main stem being of fairly uniform diameter except near the base, where it increases slightly, being about 4·1-4·5 μ. The base itself is rounded and has no plug.

* In 1951 we reported (Johnston and Angel, 1951, p. 54) that the only common xiphidiocercaria found by us in *Lymnaea lessoni* was a form with stylet 24 μ long. This is the cercaria now identified as the larva of *Plagiorchis maculosus*.

The whole surface of the body is beset with rows of tiny spines. The acetabulum is situated in the posterior half of the body.

There is an obvious pharynx, but the rest of the alimentary system is not easily seen. Sometimes there appeared to be a slight prepharynx; if this is indeed present (and not an artefact), it is, as was noted for the adult, very short. There is a short oesophagus; this, and the alimentary caeca, were very narrow when seen at all.

The excretory system is very difficult to elucidate. Treatment with intra vitam stains such as basic fuchsin in saline, improved it only slightly. The gland and cystogenous cells which occur throughout the body are sometimes extremely opaque and murky in appearance, and it is impossible to see through them. The bladder itself can generally be seen quite clearly. It is Y-shaped, and in life is continually changing shape; the upper part of the stem sometimes contracts so strongly that the bladder appears to consist of two parts, the posterior one rounded, the anterior one with short, wide arms in the form of a V. McMullen (1937) showed the main excretory vessels arising from the tips of the arms of the bladder for *Plagiorchis* spp. In the material examined here it was almost impossible to come to a decision. At one time the vessels would appear to arise terminally, at another it would seem equally certain that they were sub-terminal. It was pointed out for *P. jaenschi* (Johnston and Angel, 1951) that the twisting of the main and accessory tubes, with other factors, made the supposed point of entry of the main vessels into the bladder a matter to be regarded with some reserve. The anterior and posterior collecting vessels diverge from the main excretory tube at a point level with the middle of the acetabulum, but, of course, lateral to it. Beyond this, little detail of the excretory system was seen, with the exception of odd flame cells, as shown in Fig. 9. Refractile granules are scattered throughout the body. They are not abundant, as in some cercariae; the size is variable, some being very small. The gland cells occur in about 3 rows from just anterior to the acetabulum to midway between it and the pharynx. Laterally, and also posteriorly to the acetabulum, the body is filled with cells which stain with neutral red and faintly with methylene blue. They may be only cystogenous cells, but if this is so it seems strange that the anterior part of the body is quite free of them. These cells stain a uniform pale pink with neutral red, some of the nuclei showing a bright red. Without stain the cells appear greenish, finely granular, with clear nuclei. In the more darkly stained specimens the bladder shows up clearly as an unstained area.

The ducts of the gland cells, which showed only in the pre-acetabular region, were greenish, finely granular, and seemed to be only about three in number on each side.

The genital primordium shows after staining with neutral red as a mass of small undifferentiated cells in the region of the future cirrus complex.

The Cyst

Cercariae encysted readily in mosquito larvae.

The cysts were found most commonly in the head and the abdomen, and a few were found in the thorax. In the pupa it was difficult to determine the exact site of infection. One larvae which was examined after 48 hours with the host snail contained 117 cysts—29 in the head, 3 in the thorax, and 85 in the abdomen.

The cysts resembled those figured by Nöller and Ullrich (1927) and photographed by Strenzke (1952).

They were small, rounded and fairly thin-walled; the dark concretions in the excretory bladder were a regular and characteristic feature. The bladder showed through the cyst wall as a very dark Y or V shape, in which the arms and tail stem were short and stout.

Cysts one day old measured about 90-105 $\mu \times$ 90-98 μ, and three cysts of 20 days old (which were the largest of about 80 measured) were 106-120 $\mu \times$ 106-113 μ. The average size of 80 cysts, most of which were from 1-6 days old, was 106-100 μ.

Strenzke recorded the cysts as being usually round, seldom oval; an average of 100 cysts 128 μ in diameter, the range 102-150 μ.

The cyst described by von Linstow which was mentioned previously in this paper, was thick-walled, oval and measured 440 $\times$ 300 μ. As stated above, this was probably another species of *Plagiorchis*. According to von Linstow, Filippi gave the cyst diameter as 190 μ.

The natural secondary host is probably a chironomid, though no doubt the cercaria sometimes utilizes mosquito and other insect larvae under natural conditions. Chironomid larvae were not available in the laboratory at any of the times that infections were being tried.

Animals used in trial infections, from none of which were cysts recovered, were the crustaceans, *Daphnia* sp., shrimp (*Paratya australiense*), yabbie (*Cherax destructor*), amphipod (*Chiltonia subtenuis*); the molluscs *Lenameria* sp., *Planorbis isingi*, *Lymnaea lessoni*; 2 leeches; the fish *Gambusia affinis*, and tadpoles (*Limnodynastes* sp.).

The only other xiphidiocercaria which has been found as a parasite of *Lymnaea lessoni* in South Australia, *Cercaria Plagiorchis jaenschi* Johnston and Angel, 1951, is very similar in size and appearance to *C. Plagiorchis maculosus*. It is distinguishable in fresh material, without detailed microscopical examination, only by the size of the stylet, which is noticeably larger (34 μ) in *C. Plagiorchis jaenschi*. The gland cells are more extensive in *C. Plagiorchis maculosus*. The normal secondary intermediate host of *P. jaenschi* was thought to be the crustacean, *Cherax destructor* (in which encystation took place readily); in *Plagiorchis maculosus* encystation occurs in insect larvae, but apparently not in crustaceans.

Plagiorchis maculosus has now been recorded from a large number of birds, most of which are insectivorous, and from the rodent, *Citellus musicus planicola*. It was found in 50 per cent. of the *Citellus* examined by Schulz (1932) in what was apparently a fairly wide survey. It appears that *Plagiorchis maculosus* has no great specificity for its adult host, though the second intermediate host is very restricted. It seems likely that many species of *Plagiorchis* have been described as new largely because they occurred in unrelated hosts, and an examination of the types may indicate a large number of synonyms of *P. maculosus*.

I have been able to examine types of *P. clelandi* Johnston, 1917, and *P. spatulatus* Johnston, 1917 (Australian Museum W.435 and W.434 respectively), and was unable to find any points by which they could be separated from the Australian specimens of *P. maculosus* I have examined, and measurements of which are given in this paper.

Johnston stated that *P. clelandi* was more closely related to *P. maculosus* (Rud.) than to any other species. It differed mainly in the arrangement of the fields of the yolk glands, which in the Australian species never extended as far forwards as the fork of the intestine, and always remained separate in the posterior region. In the type specimen the follicles of the yolk glands have taken up the stain more deeply in some parts than in others; close examination of the dorsal surface shows that some follicles do extend between the two main fields and that there are even one or two follicles right in the median line. The testes are bigger than in most specimens examined, but I do not consider this justifies the placing of the species in the variety *anatis*.

The inclusion of *P. spatulatus* as a synonym of *P. maculosus* means that the lower range for size of this species must be extended. However, there seem no other differences by which to separate the two species. According to Johnston, *P. spatulatus* resembled *P. maculosus* more closely than any other species. He separated *P. clelandi* from *P. spatulatus* on a number of points, but especially in the extent of the yolk gland fields, which extended further forward, were more lateral in front of the testes and extended further in towards the middle behind them in *P. spatulatus*.

Johnston (p. 248) noted that whereas *P. clelandi*, *P. maculosus*, *P. nisbetii* were from passerine birds, *P. spatulatus* occurred in one of the Motacillidae (*Anthus australis*). He did not compare it with *P. notabilis* Nicoll, 1909, which was from *Anthus obscurus* and *Motacilla flava*. Nicoll gave as the chief diagnostic features of the species the short cirrus-pouch and the forward position of the ovary. The figure is presumably drawn from the one adult specimen from *Anthus obscurus*, which was described first, and "the main features of difference in the specimen from *Motacilla*" were then indicated. From the figure, the anterior part of the worm is contracted, and this seems enough to explain the apparent forward position of ovary and, with the fact that the cirrus is everted, the shortness of the cirrus pouch. Yamaguti (1954, p. 337) noted that the posterior extent of the cirrus pouch being subject to considerable variation in the members of this genus, does not constitute by itself a decisive criterion in specific determination.

In 1954, Horton-Smith and Long recovered 35 trematodes from the small intestine of a pullet from Scotland, which were identified as *Plagiorchis notabilis* by Dr. S. Prudhoe of the British Museum (Natural History). The metacercariae were found encysted in the larvae of chironomid and other flies.

I can find no record of where the type is deposited. It seems probable that *Plagiorchis notabilis* is a synonym of *P. maculosus*.

Nicoll (1909) described from Townsville, Queensland, *Lepoderma nisbetii* from *Chibia* (*Dicrura*) *bracteata*. Nicoll's figure is not very detailed, and he stated that the two specimens, from which the description was made, were "somewhat macerated". Nicoll did not designate a type, nor state where the specimens were deposited, but Mr. A. J. Bearup, of the Australian Institute of Tropical Medicine, has sent me two spirit specimens which are obviously the ones from which Nicoll gave his description (A.I.T.M. No. 121). Mr. Bearup tells me that the label is in Nicoll's handwriting; the details are similar to those given in the paper. One worm was in pieces, the other very dark. Though treatment with trisodium phosphate improved the intact worm, it was not in good enough condition to enable any real description to be given.

It is not possible to say that this is a synonym of *Plagiorchis maculosus*, though the differences (from the description and the figure) may well be attributable to the poor condition of the specimens. Nicoll did not name any differential characters for the species.

Yamaguti and Mitunaga (1943) stated that it seemed probable that *P. orientalis* Park (1939) from the Korean *Hirundo daurica nipalensis* was identical with *P. maculosus*. Park had distinguished it from var. *citelli* by (1) the vitellaria being confluent dorsally, and (2) the fact that the cirrus sac extended only to the posterior margin of the acetabulum.

VARIETIES OF *PLAGIORCHIS MACULOSUS*

In 1928 Skrjabin described *P. maculosus* var. *anatis*, from 1 specimen found in 1 of 2 ducks (*Casarca casarca*) from Transbaikalia. A characteristic difference between this variety and the typical *P. maculosus* was the structure of the vitelline follicles which, in the variety, were rather small individually but very closely placed, and in the typical form "plus gros, plus grands" and less thickly distributed. From Skrjabin's figure, the most obvious feature is the size of the testes, which appear relatively huge. The measurements given were 0·4 mm. diameter for each, which is appreciably larger than in any specimen previously recorded, or in any examined in the present collection. The size of the eggs, also, 36 × 22 μ, is somewhat greater than in other *P. maculosus*.

The condition of the animal, whether living, dead, compressed, etc., was not mentioned. To my knowledge, this variety has not been recorded since it was described.

Massino, in 1929, included a description of Skrjabin's specimen. His paper has an obvious mistake in labelling. His Fig. 9 which was labelled *P. maculosus* var. *anatinus*, corresponds to Skrjabin's Fig. 2 of *Plagiorchis potanini*, while his Fig. 8, called *P. potanini*, corresponds with Skrjabin's Fig. 1 of *P. maculosus* var. *anatis*.

Mehra (1937), who had apparently seen Massino's figures and not Skrjabin's, transferred *Lepoderma maculosus* var. *anatinus* to a new species, *L.* (*Multiglandularis*) *russii* on the grounds that it did not belong to the subgenus *Plagiorchis*, as did *P. maculosus*. The species *P. russii* is thus invalid, being a synonym of *P. potanini*.

P. maculosus var. *citelli* was described by Schulz in 1932 from the rodent *Citellus musicus planicola*. Schulz stated that it did not really differ from the typical *Plagiorchis maculosus* described in 1802, or from Skrjabin's *P. maculosus anatis* (from a duck); on the other hand, it was very near to *P. popowi* Palimpsestow which was described from a dog and was later found by Skworzow in a pig. Schulz placed it as a separate subspecies because of its host, but thought it possible that when more material was available and the biology of the parasite better known, it might be necessary to synonymise these previously mentioned forms.

In 1939 Yamaguti described *P. maculosus motacillae* from *Motacilla cinerea caspica*. He stated that it differed from the closely related *Plagiorchis notabilis* Nicoll, 1909, *P. spatulatus* Johnston, 1917, and *P. maculosus* (Rud.), in the posterior position of the testes. From his figure, the anterior border of the anterior testis is at exactly the middle of the body. The posterior testis does appear to lie nearer to the posterior end of the body than is usual in *P. maculosus*, but this is partly due to the large size of the testes, and partly perhaps to the contracted state of the body, which is evident from the figure in the anterior region. Yamaguti did not mention *P. maculosus anatis*, in which the testes are large and extend almost as far posteriorly as in *P. maculosus motacillae*. There seems no valid distinguishing feature between these two varieties. If the large size of the testes is a uniform character, the variety *anatis* should stand, with var. *motacillae* a synonym. However, *anatis* was described from a single specimen, and Yamaguti's *motacillae* was described from only 3 specimens, 1·0-1·5 mm. long, in which the range of size for the testes was 0·15-0·31 × 0·15-0·28 mm., while the suckers varied only slightly. The size of the testes may be variable, or apparent differences may be attributable to treatment or fixation.

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TABLE 1.

PLAGIORCHIS MACULOSUS FROM BIRDS IN SOUTH AUSTRALIA.

N.B. The two specimens from *Grallina cyanoleuca* are identified only as *Plagiorchis* sp. (See text p.268.). The range of measurements for length and breadth is given; the size of organs is given as averages. Length of organs given first, width afterwards. The number of specimens in which it was possible to measure the organs is given in brackets. All specimens fixed in formalin.

Date	No. of birds infected	Host	Locality	No. measured	Fixation	Length mm.	Breadth mm.	Oral Sucker mm.	Ventral Sucker mm.	Anterior testis mm.	Posterior testis mm.	Ovary mm.
15.9.48	1	*Hirundo neoxena*	Tailem Bend	6	Flattened	1·5-3·2	·50-·85					
5.3.56	6	*Hirundo neoxena*	Wellington	10		0·9-1·8	·27-·71	·23 × ·20 (6)	·19 × ·21 (6)	·15 × ·15 (3)	·18 × ·15 (3)	·12 × ·11 (3)
18.9.40	1	*Rhipidura leucophrys*	Tailem Bend	10	Flattened	1·7-2·5	·61-·81	·26 × ·26	·26 × ·25	·25 × ·21	·28 × ·22	·17 × ·17
2.3.56	1	*Rhipidura leucophrys*	Morgan	2		0·97-1·1	·33-·37	·18 × ·18	·15 × ·15			
11.3.57	5	*Rhipidura leucophrys*	Tailem Bend	11		1·3-2·6	·48-·77	·21 × ·23	·22 × ·20	·22 × ·20	·26 × ·21	·16 × ·16
15.10.37	1	*R. flabellifera*	Tailem Bend	1		1·5	·60	·20 × ·22	·20 × ·19	·19 × ·20	·22 × ·17	·12 × ·12
8.3.44	1	*R. flabellifera*	Tailem Bend	1		1·4	·53	·20 × ·20	·22 × ·20	·23 × ·20	·26 × ·18	·18 × ·14
27.10.48	1	*R. flabellifera*	Tailem Bend	5		1·7-2·9	·67-·76	·23 × ·25	·26 × ·24	·35 × ·26 (3)	·42 × ·30 (3)	·24 × ·21 (3)
23.2.42	1	*Gymnorhina hypoleuca*	Tailem Bend	1		1·7	·55	·25 × ·25	·22 × ·22	·20 × ·18	·22 × ·17	·16 × ·17
28.2.56	4	*Pomatostomus superciliosus*	Morgan	6	Fixed, when alive, without pressure	0·8-1·5	·37-·80	·20 × ·22	·18 × ·19	·14 × ·14	·14 × ·16	·11 × ·12
				7	Fixed after death	1·1-1·9	·32-·57	·19 × ·19	·17 × ·17	·13 × ·11	·13 × ·11	·11 × ·09
7.4.55	2	Chicken (Experimental)		4		1·6-2·4	·60-·63	·25 × ·25 (7)	·22 × ·20 (7)	·24 × ·20 (3)	·25 × ·20 (3)	·19 × ·19 (3)
26.2.40	1	*Grallina cyanoleuca*	Tailem Bend	1		2·0	·75	·33 × ·37	·30 × ·28	·24 × ·20	·24 × ·18	·28 × ·22
1.6.40	1	*Grallina cyanoleuca*	Tailem Bend	1		1·6	·47	·27 × ·26	·19 × ·19	·22 × ·17	·22 × ·17	·14 × ·12

TABLE 2.

RECORDED DIMENSIONS AND HOSTS OF *PLAGIORCHIS MACULOSUS*.

Measurements in inverted commas estimated from drawings, or by converting "linies" into millimetres.
Measurements, in mm, are given to nearest decimal place; in some cases, e.g. for *P. orientalis*, approximate measurements are estimated.

Date	Author	Name	Hosts	No.	Fixation	Length mm.	Breadth mm.	Oral Sucker mm.	Ventral Sucker mm.	Anterior Testis mm.	Posterior Testis mm.	Ovary mm.	Eggs Length microns	Eggs Breadth microns
1802	Rudolphi	*Fasciola maculosa*	*Hirundo rustica*	—	—	"2·1"	"0·5-0·7"							
1902	Braun	*Plagiorchis maculosa*	*Hirundo rustica*	1	—	"2·66"	"0·8"							
1909	Lühe	*Plagiorchis maculosa*	*Riparia riparia* *Delichon urbica* *Apus apus* *Hirundo rustica* *Caprimulgus europaeus*			2·0-2·5	0·5-0·7	·20-·30	·15-·20					
1928	Skrjabin	*P. maculosus* var. *anatis*	*Casarca casarca*	1		2·2	0·75	·23 × ·25	·25	·40 × ·40	·40 × ·40	·22 × ·24	36	22
1932	Schulz	*P. maculosus* var. *citelli*	*Citellus musicus planicola*			2·0-2·6	·96-1·00	·25-·30 × ·26-·28	·30-·31 × ·26-·32	·29-·25 × ·28-·26	·33-·27 × ·28	·29-·27 × ·25-·27	30-34	19
1935	Yamaguti	*P. maculosus*	*Hirundo rustica gutturalis*	3	—	1·60-1·92	·57-·70	·20-·25	"same"	-·25	-·25	·16-·22 × ·14-·16	32-36	20-24
1939	Yamaguti	*P. maculosus*	*Hirundo rustica gutturalis* *H. daurica nipalensis*	?	Fixed in acetic sublimate under slight cover-glass pressure.	1·6-3·9	·56-1·25	·20-·34	·20-·35	·22-·50 × ·18-·43		·16-·34 × ·13-·30	30-39	18-24
1939	Yamaguti	*P. maculosus* var. *motacillae*	*Motacilla cinerea caspica*	3	—	1·0-1·5	0·4-0·6	·16-·18	·13-·15	·15-·31 × ·15-·28 (subglobular)		·10-·19 rounded	30-33	18-19
1943	Yamaguti	*P. maculosus*	*Hirundo rustica gutturalis*	6	—	1·6-1·8	·52-·60	·22-·25 × ·21-·25	·19-·24 × ·20-·25	·20-·25 × ·20-·26		·15-·18 × ·17-·20	30-34	18-21
			Parus atricapillus restrictus	4	—	2·2-2·5	·75-1·00	·19-·30 × ·20-·30	·21-·30 × ·21-·30	·21-·35 × ·20-·35		·20-·28 × ·28-·29	33-39	18-21
1946	Callot	*Lepoderma maculosum*	*Apus apus*	1	Living	2·5	0·80	·30	·32	·34 × ·30	·35 × ·26	·30		
				1	Same specimen fixed.	2·35	0·85	·30	·25				30-32	20
1952	Strenzke	*P. maculosus*	*Aidemosyne cantans*	"30"	mature, with eggs with only few eggs	1·6-2·0 1·1-1·4	0·5-0·8 0·1-0·2						34-37	21-23
1909	Nicoll	*P. notabilis*	*Anthus obscurus*	1	—	1·6	·57	·20 × ·18	·16 × ·16	·25 × ·16	"About same"	·16 × ·12	31	19
			Motacilla flava	1	—	1·4	—	·17 × ·16	·14 × ·13	·19 × ·15	·17 × ·15	·11 × ·10	31	21
1914	Nicoll	*P. nisbetii*	*Chibia bracteata*	2	"Somewhat macerated"	1·25	·40	·22 × ·24	·15 × ·14	·1 long "Elongate oval"	"Slightly larger"	·11 × ·11		
1916	Johnston, S. J.	*P. spatulatus*	*Anthus australis*		Balsam mount	* ·80-·99	·35-·39	·16	·13	·14 × ·12	·14 × ·12	·08	29-33	17
1916	Johnston, S. J.	*P. clelandi*	*Petrochelidon ariel*	1	Balsam mount	*2·2	·65	·29 × ·25	·25	·31 × ·29	·37 × ·29	·17 × ·23	30-33	17-22
1939	Park	*P. orientalis*	"Swallow"	3	—	1·5-1·7	·69-·75	·23 × ·23	·23 × ·24	·26 × ·26	·28 × ·22	·16 × ·20	28-34	14-19

* Type specimens. In the case of *P. spatulatus*, the range of length and breadth is given for an unspecified number of worms; the type was 0·99 mm. × 0·39 mm.